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DEVELOPMENT OF *AMPHIOPLUS ABDITUS* (*VERRILL*) (ECHINODERMATA: OPHIUROIDEA). II. DESCRIPTION AND DISCUSSION OF OPHIUROID SKELETAL ONTOGENY AND HOMOLOGIES [1]

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The descriptive studies of the last century, meticulous and seemingly irrefutable, sometimes conceal serious flaws. The comprehensive scheme of ophiuroid skeletal anatomy of Ludwig (1878, 1881, 1899, 1901), for example, is presented in numerous treatises (*e.g.*, Bather, Gregory, and Goodrich, 1900; MacBride, 1906; Cuénot, 1948; Hyman, 1955; Spencer and Wright, 1966) as a cornerstone for theories of echinoderm systematics and phylogeny. In the present paper, Ludwig's deductions and observations on ophiuroids are compared and contrasted with aspects of the anatomy and ontogeny of *Amphioplus abditus*, and a new interpretation of the ophiuroid skeleton is suggested. In addition, it is shown that juveniles of *A. abditus* undergo such drastic changes in skeletal morphology during ontogeny, that different developmental stages might easily be mistaken for the young of other genera. The implications of these transformations for systematics of the amphiurids are considered. Terminology employed for this treatment is based on accepted names of structures in the adult ophiuroid, except for "buccal scale" (*cf.*, Hyman, 1955; Thomas, 1962). The nomenclature and abbreviations are summarized in Figure 1.

Materials and Methods

Amphioplus abditus is a burrowing amphiurid with direct development. Its demersal, lecithotrophic embryos develop within a fertilization membrane that rests on the sediment (Hendler, 1977). Specimens were collected and treated as previously described (Hendler, 1977). Postlarval stages were reared in vessels of sediment, partly immersed in a running seawater system to maintain the cultures near field temperatures. Juveniles were collected from Beebe Cove, Noank, Connecticut, and Wild Harbor, West Falmouth, Massachusetts.

Skeletal development was studied using whole or dissected specimens which were dehydrated, cleared, and mounted in "Permount." The hard-parts were examined with both regular illumination and polarized light, and Rose Bengal or Grenacher's Borax Carmine were used to stain the water-vascular system (Humason, 1967).

Results

Larval skeleton

A triangular granule appears in both posterior angles of the 24-hour embryo, and each granule grows to a tetraradiate spicule within five hours. By 33 hours,

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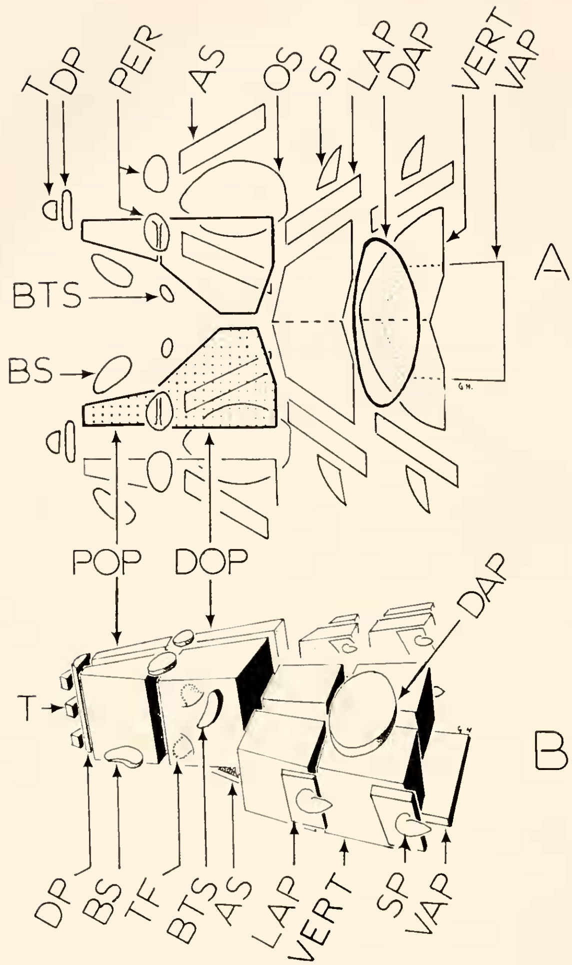

FIGURE 1. A. Diagrammatic portion of an ophiuroid jaw frame, in dorsal view with disc removed; mouth opening is to the left. The base of one arm and two half-jaws are illustrated; ambulacra of the vertebrae are separated by dashes; plates of the jaw shown as unfused pieces. Stippled area = oral plate = half-jaw = proximal oral plate + distal oral plate. B. Diagrammatic three-dimensional representation of an ophiuroid oral frame section with disc removed; mouth opening is to the left. An entire jaw and proximal bases of two arms are shown. Ambulacra of each jaw and vertebra are shown as unfused plates. The proximal and distal oral plates of the jaw are modified and abradially directed arm-vertebrae (ambulacra); ambulacral plates from *two* arms comprise each jaw. AS represents adoral shield (adambulacral-2); BS, buccal scale; BTS, first buccal tube-foot scale; DAP, dorsal arm-plate; DOP, distal oral plate (ambulacral-2); DP, dental plate; LAP, lateral arm-plate (adambulacral); OS, oral shield; PER, peristomial plate; POP, proximal oral plate (ambulacral-1); SP, arm spine; T, tooth; TF, buccal tube-foot; TP, terminal plate; VAP, ventral arm-plate; and VERT, vertebra (ambulacrum).

the four points of the spicule lengthen and give rise to lateral and terminal branches while several short, branching extensions accumulate at the nexus of the primary rods (Fig. 2). Resorption of the larval skeleton normally begins around 57 hours (Fig. 2), and between 74 and 84 hours, as the embryonic arms disappear, the

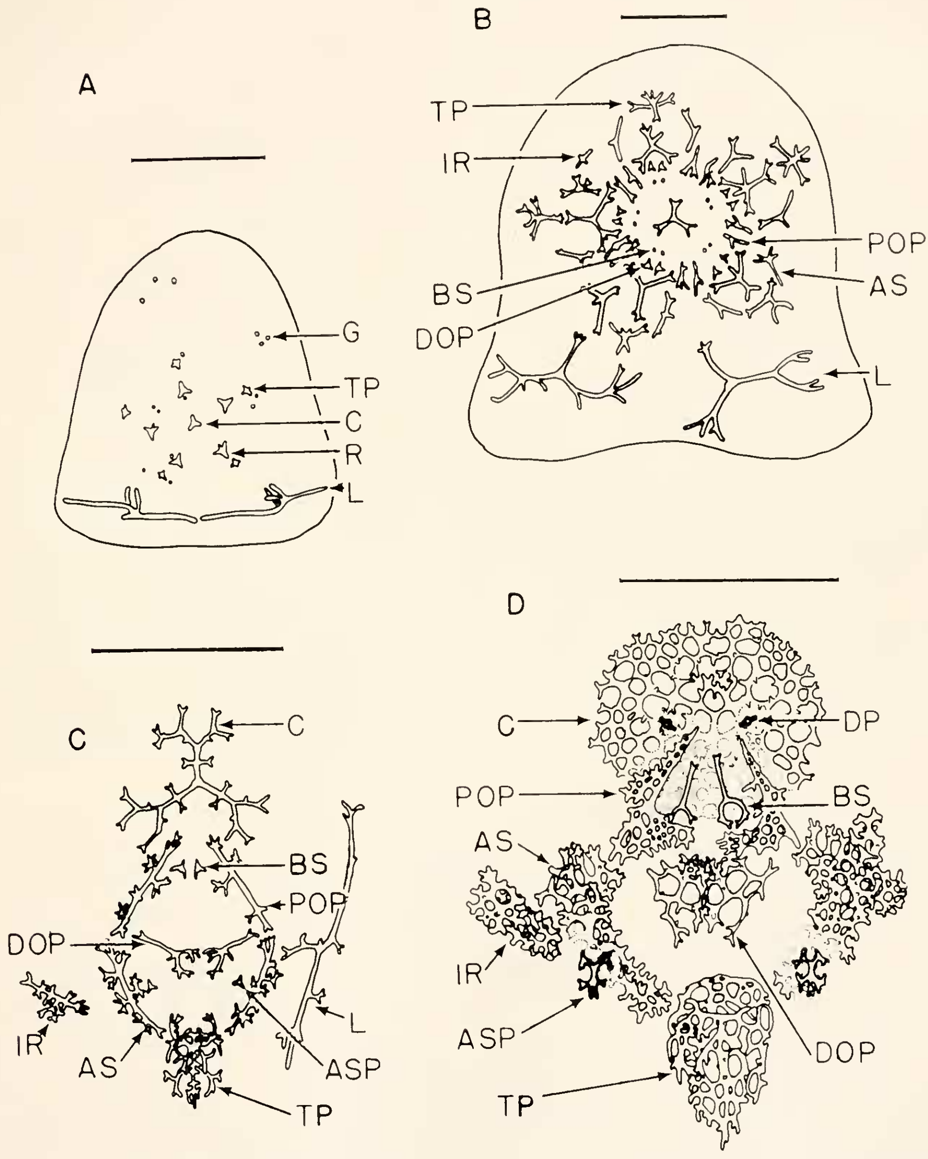

FIGURE 2. Diagrams showing approximate arrangement and relative size of developing skeletal elements (in ventral view). C and D show only one radial portion of the embryo: A, late triangular embryo, 35 hr; B, early star-disc stage, 55 hr; C, late star-disc stage, 73 hr; and D, newly hatched juvenile, 96 hr. Scale line is approximately 0.1 mm. Abbreviations as in Figure 1, and ASP represents adoral shield spine; C, central plate; G, granules of presumptive spicules; IR, interradial-1; L, larval skeleton; R, radial plate; and TP, terminal plate.

TABLE I

Chronology of skeletal element formation.

Time	Disc diameter (mm)	Aboral surface	Oral surface
35 hr		Radial plates, central plates, terminal plates	
35–42 hr			Adoral shields, proximal oral plates (POP)
45–55 hr			Distal oral plates (DOP)
48 hr			Interradial 1 (initial)
74 hr			Adoral shield spines
84 hr			Dental plates
96–147 hr			Interradial-1 (2nd-5th)
117 hr			Ventral arm-plate-1 (VAP)
110–147 hr	0.3		Teeth
55 days			Lateral arm-plate-1 (LAP)
55–72 days			Vertebrae, lateral arm-plate spines, ventral arm-plate-2
Number of arm segments			
2–3 (<5 months)	0.4		Dorsal arm-plate-1 (DAP), madreporite, oral shields
3–4 (8 months)		Radial shields	
5	0.7	Interradial-2	Infradental papillae, ventral disc scales
7		Peristomials	Second teeth
8			First buccal tube foot scales
9	0.9		Genital scales
15			Genital plates
17	1.1		Third oral papillae, fourth oral papillae (from adoral shield spines)
20	1.3		
>30	1.6		
≫30	1.9	Interradial muscle scales, dorsal disc scales	Tentacle scales, accessory scales
>41	2.3		
≫38	2.5		
82	3.5		

branched skeletons dwindle to straight pieces with furcate tips and then are lost (Fig. 2).

The larval skeleton of *Amphioplus* compares with that of the typical ophiopluteus, the four major branches corresponding to the body, posterolateral, anterolateral and postoral rods of planktonic ophiuroid larvae. The body rods of *A. abditus* bear branched tips which may be homologous to transverse and end rods, even though the tips do not articulate. However, the general shape and pattern of secondary branching of the skeleton varies between specimens, and for each individual the skeleton in one arm is larger or more complex than its counterpart in the other arm.

It is noteworthy that by 35 hours of development separate portions of the larval skeleton, but not the ophiuroid skeletal elements, have distinct and different angles of extinction under polarized light. In other words, a larval skeletal element, which grows from a tetraradiate spicule, does not act as a single calcite crystal but is composed of irregular segments with different crystallographic orientations. This condition, unusual for echinoderm skeletons, may be an effect of a peculiarity in the coordination between the skeleton-depositing cells.

Ophiuroid skeleton

Between 30 and 35 hours, the radial, central, and terminal plates appear and regroup from a sagittal plane to form concentric rings on the ventral surface of the embryo (Fig. 2, Table I). Judging from the relative size (breadth rather than mass) of the spicules in slightly older specimens, the radial, central and terminal plates are produced in that order.

Minute, granular rudiments of the proximal oral plates and adoral shields are visible by 35 hours (Fig. 2). By 42 hours the adoral shield rudiments are larger than the proximal oral-plate rudiments, and the spicule is triradiate. Some 45-hour specimens have granular rudiments of the buccal scales and the distal oral plates.

By 55 hours the embryonic ophiuroid rudiment is pentaradiate, and its skeletal plates are arranged as successive stacks of concentric rings. In the dorsal-most plane are central and radial plates; terminal plates, shaped like stick figures with outstretched arms, are more ventral and on the perimeter of the disc; the branched proximal oral plates and adoral shields are, respectively, proximal and distal to the center of the disc and at a level below the terminals; and buccal scale granules and triradiate distal oral plates are near the ventral surface (Fig. 2).

In some specimens, after 45–55 hours of development, a single triradiate spicule, a rudiment of the initial aboral interradial plate (interradial-1), appears at the edge of the ophiuroid rudiment, ventral to the terminal plates and at the right side of the embryo in the interradius anterior to the right larval skeleton. Interradial-1 plates do not appear in the other four interradii until 96 hours of development.

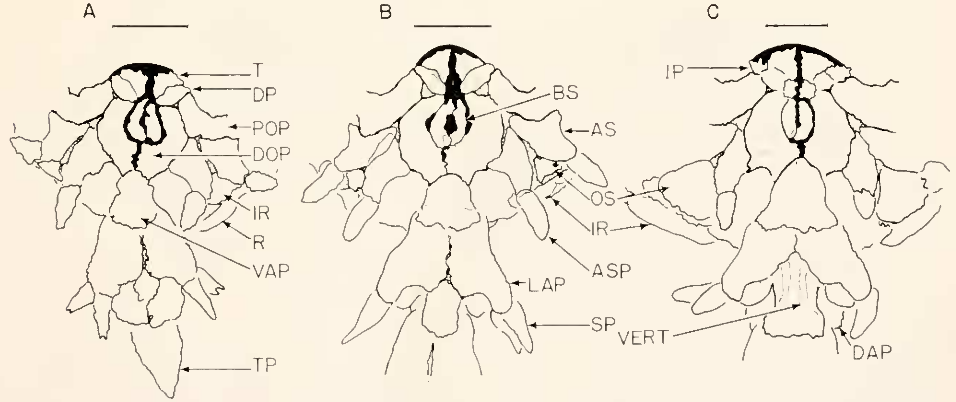

FIGURE 3. Portion of the disc, in ventral view, for different stages of development: A, 1-2 arm-segment stage; B, 3 arm-segment stage; and C, 5 arm-segment stage. Abbreviations as in Figures 1 and 2; and IP represents infradental papilla; R, radial plate. Scale line is 0.1 mm. Dotted lines separate DOP and POP as seen in polarized light.

Triradiate rudiments of the adoral shield spines appear at 74 hours, and by 84 hours the dental plates materialize as spicules proximal to the five jaws (Figs. 2 and 3). From 90 to 110 hours the skeletal elements of hatching juveniles become denser and approach their final form (Figs. 2 and 3).

By 96 hours, there are triradiate spicules, rudiments of the first interradial plates, in a plane beneath the radial plates (except for the radius with a precocious interradial-1). By 147 hours, these spicules form small plates with multiple branches; by 23 days they are larger and nearly perpendicular to the radial plates, and they then migrate to the dorsal surface of the disc.

The adoral shield spines move to the shield and grow beyond the edge of the disc. At the time of hatching, the juvenile has its dorsal surface shingled by a rosette of overlapping primary plates and around the disc there are spike-like, protruding terminal plates and adoral shield spines. Shortly before hatching (about 167 hours) on the ventral surface of the disc, the distal end of the proximal oral plate enlarges and fuses with the distal oral plate (the net-like stereom of the latter remains distinctive even after fusion). Pairs of oral plates articulate to form jaws by 230 hours.

Several days after hatching (by 196 hours) the first series of teeth, initially sparsely-branched triradiate spicules, form at the proximal surface of the dental plate, but they do not take their final massive, blunt-tipped form until the 9 to 17 arm-segment stage of development.

Rudiments of the ventral arm-plates, already present at 117 hours, become dense, fenestrate plates with an elongate pentagonal shape by 13 days. Opacity of the ventral arm-plates and the appearance of lateral arm-plates by 55 days obstruct examination of the vertebrae, although slender, unfused vertebral ossicles are still discernable until 72 days when the first arm spines and second series of ventral arm-plates appear. The first dorsal arm-plates are added to the arm before three months.

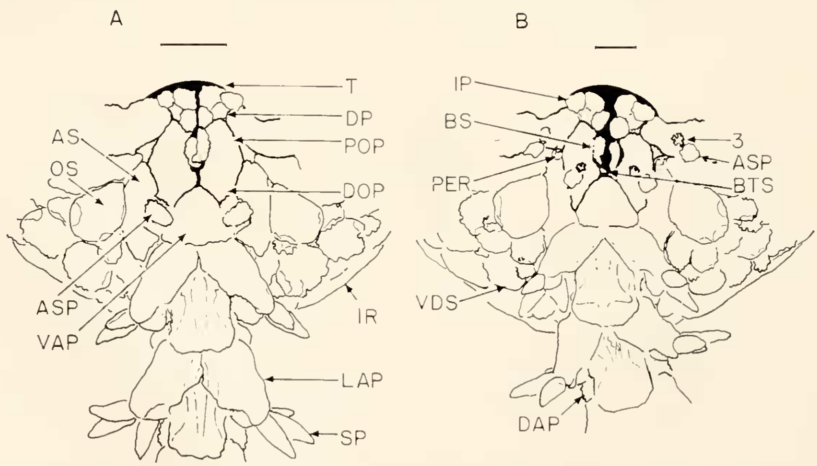

FIGURE 4. Portion of the disc,, in ventral view, for different stages of development: A, 9 arm-segment stage; and B, 17 arm-segment stage. Abbreviations as in Figures 1 to 3; and 3 represents third oral papilla; VDS, ventral disc scales. Scale line is 0.1 mm. Dotted lines separate DOP and POP.

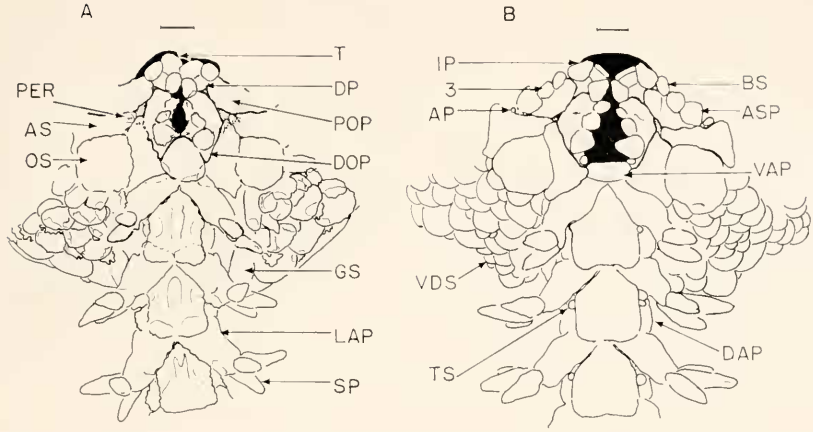

FIGURE 5. Portion of the disc, in ventral view, for different stages of development: A, 21 arm-segment stage; and B, >30 arm-segment stage. Abbreviations as in Figures 1 to 4; and AP represents accessory papillae; GS, genital scale; TS, tentacle scale. Scale line is 0.1 mm. Dotted lines separate DOP and POP.

As each new arm segment is added a ventral arm-plate appears before the lateral arm-plates and arm spines, and a dorsal arm-plate finally forms to cap the segment. The arm-plates and spines take a form characteristic of the adult by the 17 arm-segment stage.

Rudiments of the oral shields and madreporite do not appear until the third arm-segment begins to form (by five months). They form *in situ* on the oral surface of the disc, proximal to the interradial-1 series (Fig. 3). Even so, the stone and pore canals associated with the madreporite are present before the two arm-segment stage. By eight months there are four arm-segments, and radial shields appear at the base of the arm, on the ventral surface of the disc.

An exact chronology cannot be assigned for subsequent skeletal developments, as they were deduced using a growth series organized from material in field collections (Table I; Figs. 3, 4, and 5). There is no important change in the armature of the disc until the 5 arm-segment stage, when pairs of infradental papillae appear distal to the dental plates (Fig. 3). The most striking superficial change at this time is the addition of minute scales on the ventral surface of the disc, which separate the oral shields and interradial-1 plates. Interradial-2 plates erupt between the radials, isolating the radial plates from the interradial-1 on the dorsal surface of the disc (Figs. 3, 4, and 5). The central primary plate and the radial plates continue to grow until the disc diameter is 5 mm and then diminish in size with further growth. This allometric pattern is species-specific (Hendler, 1973).

There are three important series of minute plates within the disc. Reticulate peristomial plates are added by the 7 arm-segment stage on the inner surface of the jaw between the proximal and distal oral plates (Fig. 6). They probably arise as single spicules at an earlier stage, but there is no doubt that the peristomial plates and buccal scales are present at the same time (Fig. 6). By the 8 arm-segment stage, pairs of tiny plates form within the disc, distal to the buccal scales, and just proximal to each first ventral arm-plate. These plates will be referred to below as

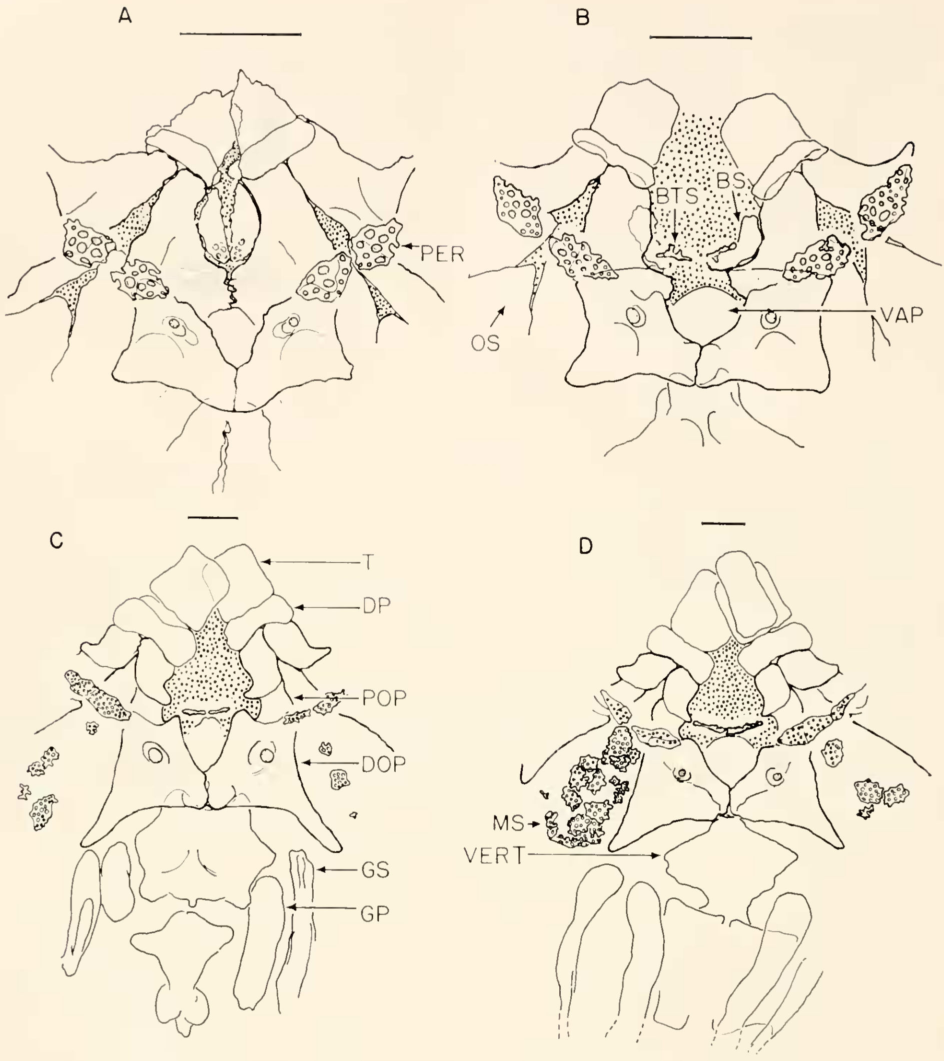

FIGURE 6. Portion of the oral frame, in dorsal view, with disc removed, for different stages of development: A, 7 arm-segment stage; B, 13 arm-segment stage; C, >30 arm-segment stage; and D, >41 arm-segment stage. Abbreviations as in Figures 1 to 4; and GP represents genital plate; GS, genital scale; MS, interradial muscle scale. Scale line is 0.1 mm. Note that buccal scales, which lie on the oral surface, cannot be seen in C or D. Dotted lines separate DOP and POP.

the first buccal tube-foot scales (corresponding plates have been treated as ventral arm-plates or homologues of ambulacral plates by various authors).

By the 9 arm-segment stage, due to growth of the adoral shield, the adoral shield spine sits near the center of the shield plate (Fig. 4). It then acts as a "tentacle scale" for the second buccal tube-feet, analogous to the minute plates on the ventral surface of the arm that shield the contracted tube-feet (tentacles). The buccal scales transform from crescentric scales to blunt spines. The madreporite exhibits an external perforation for the hydropore. The genital scales were seen in a 9 arm-segment individual; and genital plates were seen in a specimen of 15 arm-segments, but, undoubtedly, both originated at an earlier stage.

By the 17 arm-segment stage the rudiments of the third oral papillae appear on the distal surface of the oral plates (Fig. 4). The spines of the adoral shield migrate to form additional oral papillae (the fourth oral papillae). Thus, by the 21 arm-segment stage, each row of oral papillae consists of a block-like infradental followed by a spine-like papilla (formed by a buccal scale), a third papilla (chronologically the youngest), and a large distal papilla (formed by an adoral shield spine) (Fig. 5). Oral shields of adjacent jaws are initially tightly appressed, but the first ventral arm-plates, which begin migrating into the buccal area by the 5 arm-segment stage, spread apart the adoral shields.

When more than 30 arm-segments have formed, the oral plates begin to take a definitive shape with enlarged lateral extensions for the insertion of the external interradial muscles and a deep cleft for the water-vascular ring (Fig. 6). In addition, a scattering of small thin plates accumulates on the surface of the interradial muscles (Fig. 6). The paired peristomial plates lengthen and then degenerate (or even fuse?), becoming fragile scales like those on the interradial muscles. The rudimentary skeletal elements proximal to the ventral arm-plates (first buccal tube-foot scales) form reticulate pieces perpendicular to the axis of the arm. By this time tentacle scales have appeared on many arm-segments, one scale per tube-foot.

The first buccal tube-foot scales located within the oral cavity surpass the size of the peristomial plates; in larger specimens they form thin, boomerang-shaped elements beside the inner oral papillae. While the peristomial plates stop growing and/or degenerate, the scales over the interradial muscles grow larger and more numerous, obscuring the peristomials. The interradial muscle scales finally form a medial band on the muscles in the adult (especially dense on the muscle above the madreporite) (Fig. 6).

On the dorsal surface of the disc, the number of tiny scales separating the primary and interradial plate continues to grow, but two series of interradial plates remain distinct. The interradial-1 plates remain on the edge of the disc until the specimens have at least 82 arm-segments (disc diameter = 3.5 mm), and in larger animals they are left on the dorsal surface of the disc as the rate of disc growth increases centrifugally. On the ventral surface of the disc, small accessory scales (the fifth oral papillae) form distally to the fourth oral papillae, and additional accessory scales may appear in later stages of growth (Fig. 5).

Discussion

The derivation of the oral frame and the armament of oral papillae bordering the buccal cavity are discussed in detail, as these are the features of *A. abditus* that best illustrate the systematics of amphiurids (the largest family of ophiuroids) and the affinities of the echinoderm classes. The apical rosette of primary plates, radial shields, and the madreporite will be discussed first, since these structures figure prominently in evaluations of echinoderm phylogeny.

In the ophiuroids the larval skeleton plays no part in the formation of the apical system (central and radial primary plates), since the larval skeleton of ophiuroids is resorbed, as in *A. abditus,* or sometimes "discarded" (Mortensen, 1931; Olsen, 1942; Hendler, 1975). In echinoids, on the other hand, the larval skeletal pieces generate the genital and terminal apical plates (Onoda, 1931). The origin of both the larval skeleton and apical plates has been thought to provide evidence for a close affinity between the echinoids and ophiuroids. However, the divergence seen in the ontogeny of ophiuroids and echinoids implies that there is nonhomology of the larval skeleton and/or the apical plates of the two classes.

Regardless of discrepancies in homology between ophiuroids and echinoids, the central plate of ophiuroids appears to be homologous to the central plate of asteroids. Apart from this characteristic, the similarities between the discs of ophiuroids and asteroids are few. Prominent structures of the ophiuroid disc, such as radial shields, oral shields, and genital plates and scales, seem to be ophiuroid specializations without homologues in asteroids.

Each radial shield (and the other major skeletal elements) of *A. abditus* and other ophiuroids originates from a single element (not by fusion of scales as suggested in Spencer and Wright, 1966). The radial shields (and genital plates and scales) reappear when the disc of *Amphioplus* regenerates, but the primary plates (loci of disc scale formation) never are replaced (personal observation). This morphogenetic difference between the central plate and radial shields indicates that the primary plates of ophiuroids are atavistic structures that are recapitulated during ontogeny but are not necessary for the growth of the disc.

Even structures, such as the madreporite, which have been judged to show close affinities between the ophiuroids and asteroids, point up differences between the classes. Although in the recent ophiuroids an oral shield acts as the madreporite, some primitive ophiuroids possess a madreporite but lack oral shields (Spencer and Wright, 1966). It is possible that a madreporite formed of an oral shield is an innovation in the recent ophiuroids, but a different structure held the water-pore in the ancient ophiuroids. In other words, the madreporites may be nonhomologous in recent ophiuroids, ancient ophiuroids, and asteroids. Furthermore, the "precocious interradial" plate and early formation of the hydroporic canal observed in *A. abditus* could be vestiges of the primitive madreporite.

The madreporite of asteroids is usually dorsal, and ophiuroids generally have a ventral madreporite. Hence, the relationship of these two classes has been gauged by comparing the point of origin of the ophiuran madreporite: whether on the ventral hemisome (indicating lack of affinity with asteroids), or by way of migration from the dorsal surface (indicating a close relationship) (Ludwig, 1881; Mortensen, 1912, 1921; Murakami, 1940, 1941). In fact, all recent ophiuroids reported to have a ventrally migrating madreporite may actually have a "precocious interradial." For example, Murakami (1940) described a dorsal to ventral migration of the madreporite in *Axiognathus* (= *Amphipholis*) *squamatus,* but his illustrations show that the "madreporite" is identical to the "precocious interradial" of *A. abditus;* so the true madreporite of *Axiognathus* must originate at its final, ventral location. This suggests that formation of the madreporite *in situ* on the ventral surface is a characteristic distinguishing recent ophiuroids from asteroids. But, without more information, the precocious interradial of ophiuroids cannot be considered a homologue of the interradial plate, which acts as a madreporite, in recent asteroids.

Just as the superficial structures of the disc discussed above, such as the apical plates, radial shields and madreporite, suggest drastic distinctions between classes of echinoderms, basic differences in the formation of the oral frame further emphasize the divergence between ophiuroids and asteroids. In the ophiuroid embryo the oral frame is produced by a rearrangement of the paired, serial, skeletal elements that fuse to form "vertebrae" inside each arm. At the base of the arm, instead of forming vertebrae, the elements fuse with corresponding pieces in the neighboring arm, making a connecting bridge between adjacent arms that projects into the oral cavity as a tooth-bearing jaw. Half of each bridge is an "oral plate" comprised of elements from a single arm. Each jaw consists, in effect, of two oral plates (half-jaws) and accompanying elements from two contributing arms.

In his studies of this oral frame system, Ludwig (1878, 1881, 1889, 1901) homologized the ophiuroid and asteroid oral frames. He considered the proximal oral plates of the ophiuroid jaw (the proximal portion of each half-jaw) to be the first adambulacral plates, the adoral shields as the second adambulacrals, and the lateral arm-plates as serially analogous adambulacrals. He described the fusion of the proximal and distal oral plates during ontogeny and claimed the distal oral plates to be the second ambulacrals, serially homologous to the vertebrae of the arm. Ludwig believed the peristomial plates developed from the early-forming buccal scales and felt they represented the first ambulacrals of the jaw. This relationship between the peristomial plates and the buccal scales, and their identification as the first ambulacral plates, are both erroneous. Consequently, Ludwig's analogies between ophiuroid and asteroid jaws are not legitimate.

Zur Strassen (1901) pointed out that the peristomials (0 to 3 in number in different species) were not paired in each jaw as proper ambulacrals must be. Moreover, he observed that buccal scales, which Ludwig proposed to be the rudiments of peristomial plates, were present concurrently with, and hence unrelated to, peristomial plates. In the species that zur Strassen studied, the peristomials persist and the buccal scales are resorbed. In contrast, in *A. abditus* the peristomial plates are lost and the buccal scales become oral papillae. These observations indicate a basic flaw in Ludwig's scheme, calling into question the identity of the first plate of the ambulacral series and the affinities of the oral plate elements and buccal scales.

Just as Ludwig proposed, the adoral shield is adambulacral and serially homologous with the lateral arm-plates, as indicated by its position in relation to the arm and its transitory possession of a spine (Simroth, 1876; Fewkes, 1887; Murakami, 1937). The distal oral plate, clearly associated with the water-vascular system, is obviously an ambulacral plate, but the identity of the proximal oral plate is an unresolved problem. Here it is suggested that the proximal oral plate, rather than the peristomial, is the first ambulacral plate of the jaw.

Alone, the association of two pairs of tube-feet with the jaw indicates that two elements of the oral plate are ambulacral, and there are only two parts of the jaw *per se,* the proximal and distal oral plates. The attachment of the proximal oral plate in a series with the distal oral plate suggests that it is an ambulacral element, but the buccal tube-feet of *A. abditus* penetrate only the distal oral plate, suggesting that the proximal oral plate is not ambulacral. But, just as the adoral shields are homologous to lateral arm-plates, although the orientations of the shields and plates are different, the obliquely oriented proximal oral plates may be ambulacral even though they are bypassed by the water-vascular system. The separation of the proximal oral plate and the water-vascular system may simply result from the formation of buccal tentacles in reverse order in *A. abditus* and other ophiuroids (Müller, 1851; Krohn, 1851; Apostolides, 1882; Grave, 1900; MacBride, 1906; Mortensen, 1921; Fell, 1941, 1946) and the inward migration of the buccal scales and marked dorsal rotation of the ventral arm-plates.

Thus, the jaw of ophiuroids must constitute two transformed arm-segments which are highly modified and "incomplete." In the first "segment" there is an ambulacral proximal oral plate, but the identity of the adambulacral plate is problematical, and homologues of accessory plates are lacking. The second "segment" consists of the distal oral plate (ambulacral), adoral shield (adambulacral), and the ventral arm-plate. There seems to be no unequivocal homologue of the adambulacral-1 in the oral frame of recent ophiuroids. As explained above, the peristomial plates are obviously secondary structures (not adambulacrals). The buccal scales, however, might be adambulacrals, but without corroborating evidence they cannot be considered a homologue of the adambulacral plates in the first modified arm-segment. The occurrence in primitive ophiuroids of a typical jaw structure, and the presence of two pairs of oral tentacles and a modified proximal oral plate (Sollas and Sollas, 1912; Schuchert, 1915; Spencer, 1951), demonstrate both the ambulacral nature of the proximal oral plates and a basic class-wide concord in ophiuroid jaw morphology. Besides the ambulacral affinity of the proximal oral plate, the fossil record suggests a recent origin for the peristomial plates and the buccal scales, as oral papillae and buccal scales appear to be absent in ophiuroids prior to the Silurian (Spencer and Wright, 1966). Such negative evidence must be weighed against the high probability of preservational bias, especially when minute elements such as these papillae are concerned.

The ambulacral nature of the proximal oral plate makes the ophiuroid jaw arrangement consistent with that in the "somasteroid" taxa, while in other asteroids the proximal element of the jaw is an adambulacral homologue (Fell, 1963; Turner and Dearborn, 1972). Besides this major contrast between the classes, differences, such as the fusion of different ambulacrals—numbers two and three in somasteroid forms (Fell, 1963), numbers one and two in the ophiuroids—and no fusion in the asteroids, also reflect the considerable divergences between ophiuroids and asteroids. Clearly, in light of the differences in homology of the oral frame, the differences in ontogeny and morphogenesis of the madreporite and primary and interradial plates, and the unique structures of ophiuroids such as radial shields and genital plates and scales, the relationship of asteroids and ophiuroids begs re-evaluation.

The examination of skeletal ontogeny has revealed discrepencies in the phylogeny of the echinoderm classes, but ontogeny of the oral armature can indicate systematic relationships within the family Amphiuridae. Therefore, before discussing the systematics of the amphiurids, the origins of the oral papillae are reviewed.

In *A. abditus* the infradental and third oral papillae and the fifth (accessory) papillae originate *in situ*. They are secondary structures (*i.e.,* not of the ambulacral-adambulacral skeletal groundwork). In contrast, the second and fourth papillae migrate to their ultimate positions while undergoing a transformation of shape and function.

The fourth (distal) papillae originate as formidable spines on the adoral shield and are used initially for locomotion and balance, but they are dwarfed and relocated during growth of the oral frame and ultimately are retained as diminutive scales on the oral plate. Adoral shield spines of other species develop as in *A. abditus,* disappear during development, or even take a peripheral position on the disc (Mortensen, 1933b; Murakami, 1941; Schoener, 1967).

In *A. abditus,* the only species of ophiuroid whose buccal scales have been traced through development to the adult stage, the buccal scales of the juvenile are among the first-formed and most prominent skeletal elements. It is remarkable that they initially close the oral gap but as their growth slows in relation to that of the oral plate, they "sink" into the oral slit and become the diminutive second oral papillae. In contrast, the buccal scales are resorbed during development in *Axiognathus* (= *Amphipholis*) *japonicus* and *Axiognathus* (= *Amphipholis*) *squamatus* (Ludwig, 1899; zur Strassen, 1901; Sollas and Sollas, 1912; Mortensen, 1912, 1913, 1933a, 1938; Murakami, 1937, 1940, 1941; Guille, 1964). Whether all ophiuroid species have buccal scales is not known.

Since the second oral papillae arise from the buccal scales in *Amphioplus,* and they differ from tentacle scales in their time of origin and mode of growth, they should not be called "oral tentacle scales" (*cf.,* A. M. Clark, 1970). The term "buccal scales" may be used for the early-forming "spoon-shaped" plates of the buccal gap whether or not they are resorbed in the adult; but the term "second oral papillae" should be used instead of "oral tentacle scales" for adult amphiurids.

It is not certain whether both sets of buccal tube-feet have tentacle scales. The accessory scales (fifth oral papillae) associated with the second buccal tube-feet, which are obviously tentacle scales, arise long after the other four oral papillae and, as the individual grows, they increase in number to a maximum of more than five per tube-foot (Hendler, 1973). There are calcareous elements, proximal to the first ventral armplates in *A. abditus* which form during the 7- to 9-arm-segment stage, that may be tentacle scales of the first buccal tube-feet. They resemble internal buccal elements described in other species (Ludwig, 1878; Mortensen, 1912; zur Strassen, 1901; Sollas and Sollas, 1912). If these elements are not tentacle scales, then the first buccal tube-feet lack scales.

From the early appearance of infradental and distal oral papillae in *A. squamatus* and the putative juveniles of *Amphioplus acutus,* it has been inferred that these species pass through an *"Amphiura"* stage (H. L. Clarke, 1914; Mortensen, 1936). Such phylogenetic speculations are vulnerable, being based on a single character which (in the case of *Amphiura* oral armature) could easily be paedomorphic or secondarily reduced. Juveniles of *Axiognathus* or *Amphioplus* may resemble early stages of *Amphiura* or even *Amphiodia,* but it cannot be assumed that these genera recapitulate an *"Amphiura* stage" before homologues of the oral papillae of all amphiurid genera are delineated.

On the basis of their oral armature, the amphiurids may be divided provisionally into two categories: those, like *Amphiura* and *Amphioplus,* with the second oral papillae located high on the oral plate; and those, like *Amphiodia* and *Amphipholis* or *Axiognathus,* that lack second oral papillae. It is shown above that the buccal scale develops into the second papilla in *A. abditus.* However, zur Strassen (1901), Murakami (1940), and others described resorption of the buccal scale in *Axiognathus* (= *Amphipholis*) species, and these findings have been confirmed in *Axiognathus squamatus* from New England (personal observation). Thus, it is predicted that *Amphiodia* and *Amphipholis* (like *Axiognathus*) resorb the buccal scales, while *Amphiura* species (like *Amphioplus*) retain the scales as the second oral papillae.

The adoral shield spines develop in different ways in different families and genera, but it would be interesting to see whether the adoral shield spines of amphiurids always become distal oral papillae, demonstrating uniformity in the ontogeny of the amphiurid jaw. The adoral shield spine of *Axiognathus japonicus* develops identically to its homologue in *A. abditus,* but whether oral papillae of all amphiurids are homologous remains to be seen. The ontogeny of *A. abditus* supports A. M. Clark's (1970) contention that *Amphioplus,* bearing five oral papillae, occupies a central position among the amphiurids such that the oral formulae of other genera are derived by a simplification of the *Amphioplus* oral armature. Further studies are needed, however, to decide whether this complex oral structure is a primitive or an advanced trait.

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Summary

1. *Amphioplus abditus* has a vestigial two-piece larval skeleton that has portions with different crystallographic orientations. The larval skeleton is resorbed and, unlike that of echinoids, it does not act as a center of formation of the plates of the adult. The major skeletal elements of the adult develop from single (usually triradiate) spicules, and there is a uniform crystallographic orientation within each plate.

2. The radial shields, adoral shields, genital plates and genital scales are ophiuroid specializations without homologues in the asteroids. Ophiuroids can regenerate radial shields but not the apical primary plates (the latter are probably atavistic structures).

3. The madreporite and oral plates, generally thought to migrate from the dorsal surface of the disc, originate *in situ* on the ventral surface of *A. abditus*. A dorsolateral plate, probably confused with the madreporite in past studies, is a precociously formed interradial-I. The formation of a "precocious interradial plate" could be a vestige of the primitive ophiuroid madreporite. In fact, the madreporites of asteroids, ancient ophiuroids, and recent ophuroids may not be homologous.

4. The origin of each of the oral papillae is described. Buccal scales, previously (and incorrectly) thought to develop into peristomial plates, form the second oral papillae in *A. abditus*. Consequently, the second oral papillae of amphiurids should not be considered "oral tentacle scales". The true tentacle scales are cryptic structures within the buccal cavity.

5. The oral papillae of the different amphiurid genera are probably homologous. Judging from differences in the oral frame, there are probably two major amphiurid groups composed of taxa which retain the buccal scales as oral papillae (*Amphioplus* and possibly *Amphiura*), and those like *Axiognathus* (and possibly *Amphipholis* and *Amphiodia*) which resorb the buccal scales.

6. A new system of homologues is suggested for the plates of the ophiuroid oral skeleton. The proximal oral plate is considered the ambulacral portion of the first modified arm-segment and buccal scales may be the first pair of adambulacrals. The distal oral plates (ambulacral), adoral shields (adambulacral), and the first ventral arm-plate (within the buccal slit) compose the second transformed arm-segment of the oral frame. This pattern of homology, together with the dissimilarities between ophiuroid and asteroid discs constitute important differences between the ophiuroids and asteroids.

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